AUSTRALOSYODON, THE FIRST PRIMITIVE ANTEOSAURID DINOCEPHALIAN FROM THE UPPER PERMIAN OF GONDWANA

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ABSTRACT. A new genus and species of anteosaurid dinocephalian, *Australosyodon nyaphuli*, is described from the *Eodicynodon–Tapinocaninus* Assemblage Zone, the lowermost biozone of the Beaufort Group in South Africa. This genus, closely allied to *Syodon*, is the first undoubted primitive anteosaurid dinocephalian from outside Russia, and indicates that the earliest therapsids were also present in the southern hemisphere.

DINOCEPHALIANS formed part of the earliest therapsid fauna of the Russian Ocher and Isheevo formations (Tchudinov 1965) and one genus has been described from the San Angelo Formation of Texas (Olson 1962). They were also present as an important part of the therapsid fauna of the Beaufort Group of South Africa (Boonstra 1969; 1971; Keyser and Smith 1978; Rubidge 1991).

The most primitive dinocephalians have been thought to be the Russian Anteosauridae (Boonstra 1971; Hopson and Barghusen 1986), although some palaeontologists consider the Estemmenosuchidae to be the least derived group (Kemp 1982; King 1988). Anteosaurid dinocephalians are found together with the earliest known therapsids in the Russian Ocher Complex (Zone I) (Tchudinov 1960; 1983), and there is a series of fragments referred to as *Eosyodon* from the San Angelo Formation of Texas (Olson 1962) (although Parrish *et al.* (1986) questioned the identification of the latter as therapsids). However, the group is far better represented in the younger rocks of the Russian Isheevo Complex (Zone II) (Orlov 1958). Until now, the only anteosaurid from Gondwana has been the very derived genus *Anteosaurus* from the Dinocephalian Assemblage Zone of South Africa. The skull of a carnivorous dinocephalian recently collected from the underlying *Eodicynodon–Tapinocaninus* Assemblage Zone is much more primitive than *Anteosaurus*, instead resembling the most primitive anteosaurids of the Russian fauna.

MATERIAL AND METHODS

In 1987, Mr John Nyaphuli of the National Museum in Bloemfontein discovered a calcareous nodule which had shattered into several pieces, all of which contained fossilized bone. All but one of the missing fragments of the nodule were found, and stuck together prior to preparation, so that the present orientation of the bones is as they were when the skull was fossilized. Eighteen months later, on returning to the locality where the fossil was discovered, the remaining portion of the nodule was found. By this stage the rest of the skull had been prepared, and it proved difficult to be sure that the newly found piece of the nodule, containing the lateral flange of the pterygoid, was precisely correctly orientated.

Preparation was undertaken by Mr Nyaphuli using compressed air driven engravers. In areas requiring finer work, in particular, the separation of the intermeshing incisors of the upper and lower jaws, acid preparation was carried out using a ten per cent solution of acetic acid. Glyptal cement was used as adhesive and, on completion of preparation, the whole specimen was thinly coated with a dilute solution of Glyptal. The specimen (NMQR 3152) is housed in the Karoo fossil

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reptile collection of the National Museum, Bloemfontein, South Africa (Institutional abbreviation: NMQR).

The right side of the skull was badly crushed prior to fossilization, but the left side is relatively well-preserved and undistorted. A lower jaw is present and was tightly appressed to the upper jaw, prior to being removed by preparation.

SYSTEMATIC PALAEONTOLOGY

Subclass SYNAPSIDA Osborn, 1903
Order THERAPSIDA Broom, 1905
Infraorder DINOCEPHALIA Seeley, 1894
Family ANTEOSAURIDAE Boonstra, 1954
Genus AUSTRALOSYODON gen. nov.

Diagnosis. As for species.

Derivation of name. Australo, southern; *syodon*, the genus of anteosaurid dinocephalian most closely related to this specimen. The name refers to the first primitive anteosaurid from the southern hemisphere.

Australosyodon nyaphuli sp. nov.

Text-figures 1–8

Derivation of name. The species is in honour of John Nyaphuli who collected the specimen.

Diagnosis. Medium sized dinocephalian. Skull high and apparently narrow. Large frontal boss situated in interorbital region and extending anteriorly down the midline as a narrow interorbital ridge. Frontal bone forming anterior border of a depression for attachment of jaw adductor musculature which is present on skull roof lateral to pineal boss and immediately anterior to the temporal fenestra. In the palate, bosses on the palatines relatively large, protrude ventrally and bear at least twelve teeth which tend to be posteriorly inclined. Pterygoid teeth on median pterygoid boss, but absent on the lateral pterygoid flange. Dental formula i5/4 c1/1 pc12–13/7. Small incipient heel present on lingual side of lower incisors, but not manifestly present on upper incisors. Canines laterally flattened, having a sharp keel on the postero-medial edge. Postcanines relatively small, laterally compressed. Upper postcanines curve posteriad, lower postcanines point upwards with their tips pointing slightly posteriorly, and have small heels on the lingual side. Crowns of posteriormost postcanine of lower jaw antero-posteriorly broadened to form crushing surface.

Holotype. NMQR 3152. Skull and mandible, left side well preserved with several teeth; right side crushed prior to fossilization.

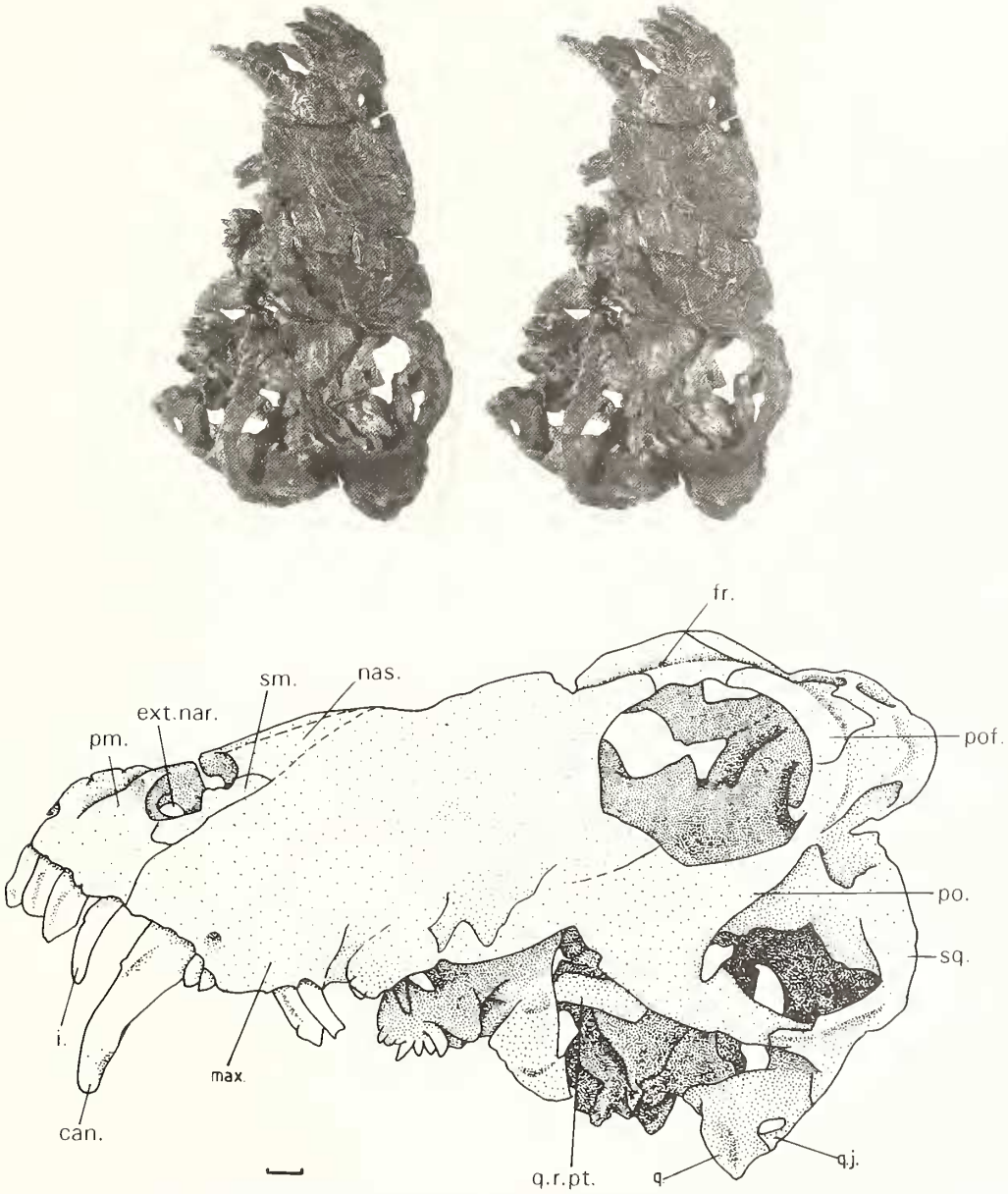
Type horizon and locality. Eodicynodon–Tapinocaninus Assemblage Zone at the base of the Beaufort Group on the farm Tuinkraal, Prince Albert Road, South Africa (map sheet: South Africa 1:50000, sheet 3321 BA Dwyka, first edition).

DESCRIPTION

The specimen, consisting of a skull and lower jaw, is more or less completely preserved. The right side has been crushed as a result of lateral compression and the zygomatic arch distorted in a medial direction resulting in the quadrate being displaced ventrally. The braincase and occiput have also been crushed.

Skull roof

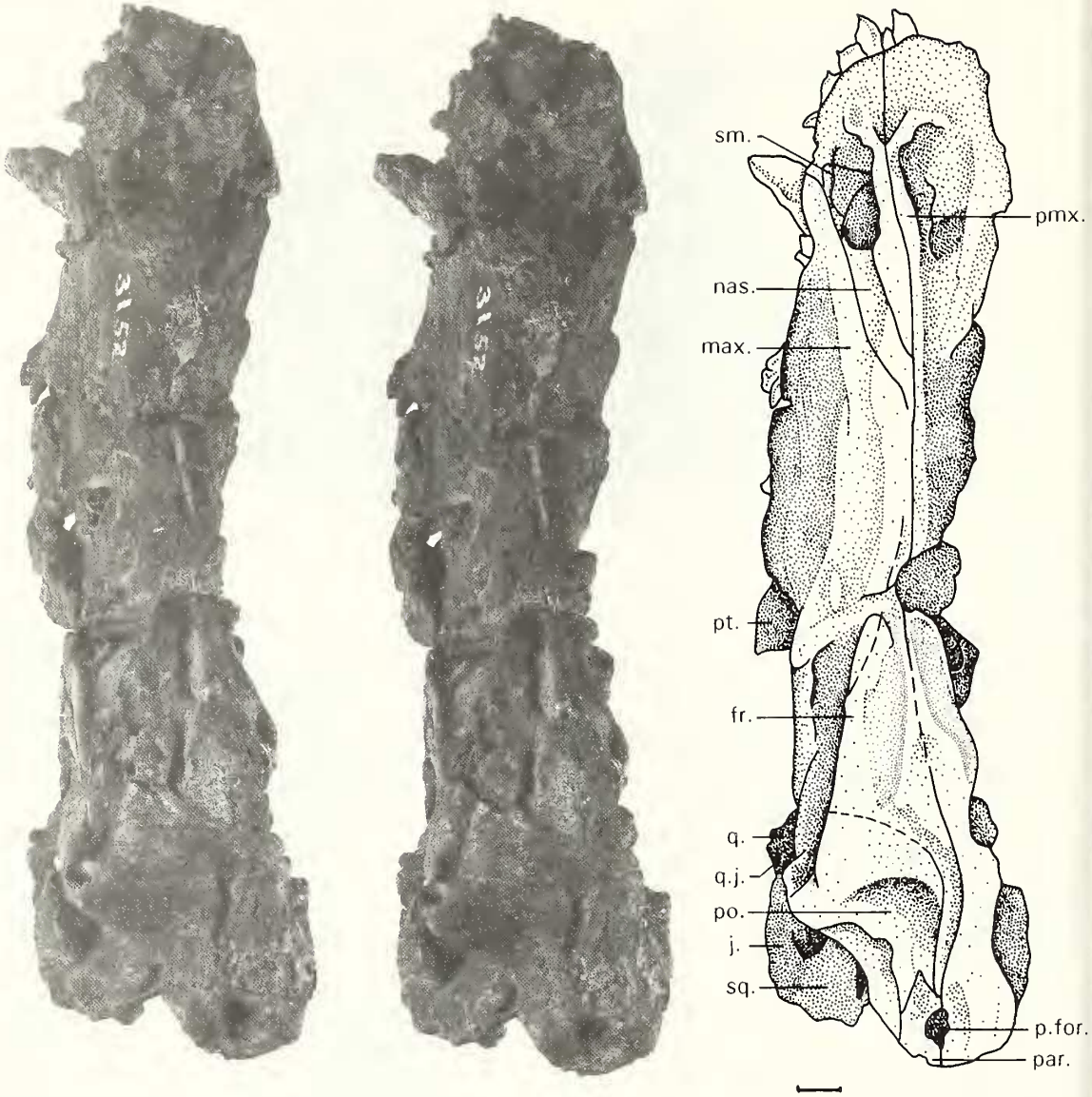
The premaxilla forms the anterior tip of the snout, and is well exposed on the lateral side of the skull (Text-fig. 1). Anterior to the canine the ventral edge of the premaxilla slopes anterodorsally. The premaxilla forms the anterior and dorsal borders of the external nares and thins as it extends postero-dorsally up the snout to



TEXT-FIG. 1. *Australosyodon nyaphuli* gen. et sp. nov.; Prince Albert Road, South Africa; *Eodicynodon–Tapinocaninus* Assemblage zone. Holotype NMQR 3152; stereophotos and diagram of lateral view. Scale bar represents 10 mm.

form a wedge-shaped contact with the nasals. A vertically orientated suture extending from the antero-ventral end of the external nares to immediately anterior of the canine, forms the contact between the premaxilla and maxilla on the lateral side of the skull.

The septomaxilla forms the floor, and the ventral portion of the posterior border of the external nares. It also extends onto the lateral surface of the skull to meet the maxilla ventrally and posteriorly, and the nasals dorsally. Posteriorly it forms a pointed contact between the maxilla and nasal bones.



TEXT-FIG. 2. *Australosyodon nyaphuli* gen. et sp. nov.; Prince Albert Road, South Africa; *Eodicynodon–Tapinocaninus* Assemblage zone. Holotype NMQR 3152; stereophotos and diagram of dorsal view. Scale bar represents 10 mm.

The maxilla forms most of the side of the snout. Dorsally it is in contact with the nasal, and appears to be in contact with the prefrontal posterodorsally, although the position of this suture is uncertain.

The anterodorsal border of the orbit is formed by the prefrontal which has been crushed on its anterior and ventral sides such that it is difficult to determine its relationship with the adjoining bones with certainty. Dorsomedially and posteriorly, the prefrontal is in contact with the frontal by means of a suture which extends anteromedially from the anterodorsal rim of the orbit at an angle of *c.* 45°. As this portion of the skull roof is weathered, it is not possible to determine the orientation of the sutures at the junction between the frontal,

prefrontal and nasal bones. The sutures between the prefrontal and lachrymal bones are unclear, as also are those between the lachrymal, maxilla, and jugal.

The frontal forms a large portion of the dorsal border of the orbit. Because of the weathered nature of the skull roof anterior to the orbits, the contact between the frontal and nasal bones is unclear. From a point in line with the anterior margin of the orbit, a prominent longitudinal ridge extends posteriorly down the midline on the skull roof along the contact between the left and right frontal bones. Almost a quarter of the way along the frontal bone, this ridge flares laterally to form a boss on the skull roof above the posterior half of the orbit. Posteriorly, this boss slopes downwards gently, and continues as a longitudinal ridge which extends almost as far as the contact between the frontal and parietal bones (Text-fig. 2).

The suture forming the border between the frontal and postfrontal bones extends medially from the posterodorsal border of the orbit. Close to the midline, it curves in a posterior direction to meet the suture between the parietal and postorbital bones. The frontal thus continues posteriorly to form a narrow 'finger' between the postfrontal on the lateral side and the parietal medially. This narrow projection is not present in *Titanophoneus*, and in *Syodon* the author was not able to recognize the suture between the postorbital and postfrontal bones.

The sutural contact between the postfrontal and postorbital bones extends in a medial direction from the posterodorsal portion of the orbit. Close to the midline of the skull, the suture turns posteriorly towards the pineal foramen so that the postfrontal forms a pointed contact between the postorbital on the lateral side and the parietal on the posterior and posteromedial sides. This suture continues posteriorly on the dorsal portion of the zygomatic arch as the contact between the postorbital and parietal bones.

The parietal forms a narrow border around the anterior side of the pineal foramen. Anterolateral to the pineal foramen, this bone forms a wedge-shaped contact with the frontal; it meets the postfrontal anterolaterally, has a long sutural contact with the postorbital laterally and posterolaterally, and meets the tabular and interparietal on the posterior and posteromedial sides respectively (Text-fig. 2). The outer surface of the posterior region of the parietal is weathered but it appears to form a large proportion of the dorsal portion of the occipital plate on the posterior side of the skull.

The postorbital bone, which is not greatly pachyostosed, forms the entire posterior and posteroventral border of the orbit, as well as the dorsal border of the temporal fenestra. The suture between the postorbital and jugal bones on the posteroventral side of the orbit could not be determined.

The squamosal forms the posterodorsal and posterior borders of the temporal fenestra, and meets the jugal on the ventral margin of this opening. This contact is not clear. The skull is broken on the dorsal side of the temporal opening so that the contact between the postorbital, and squamosal is unclear. The jugal forms a portion of the ventral border of both the temporal fenestra and the orbit. The exact limits of this bone are uncertain as the sutures could not be determined.

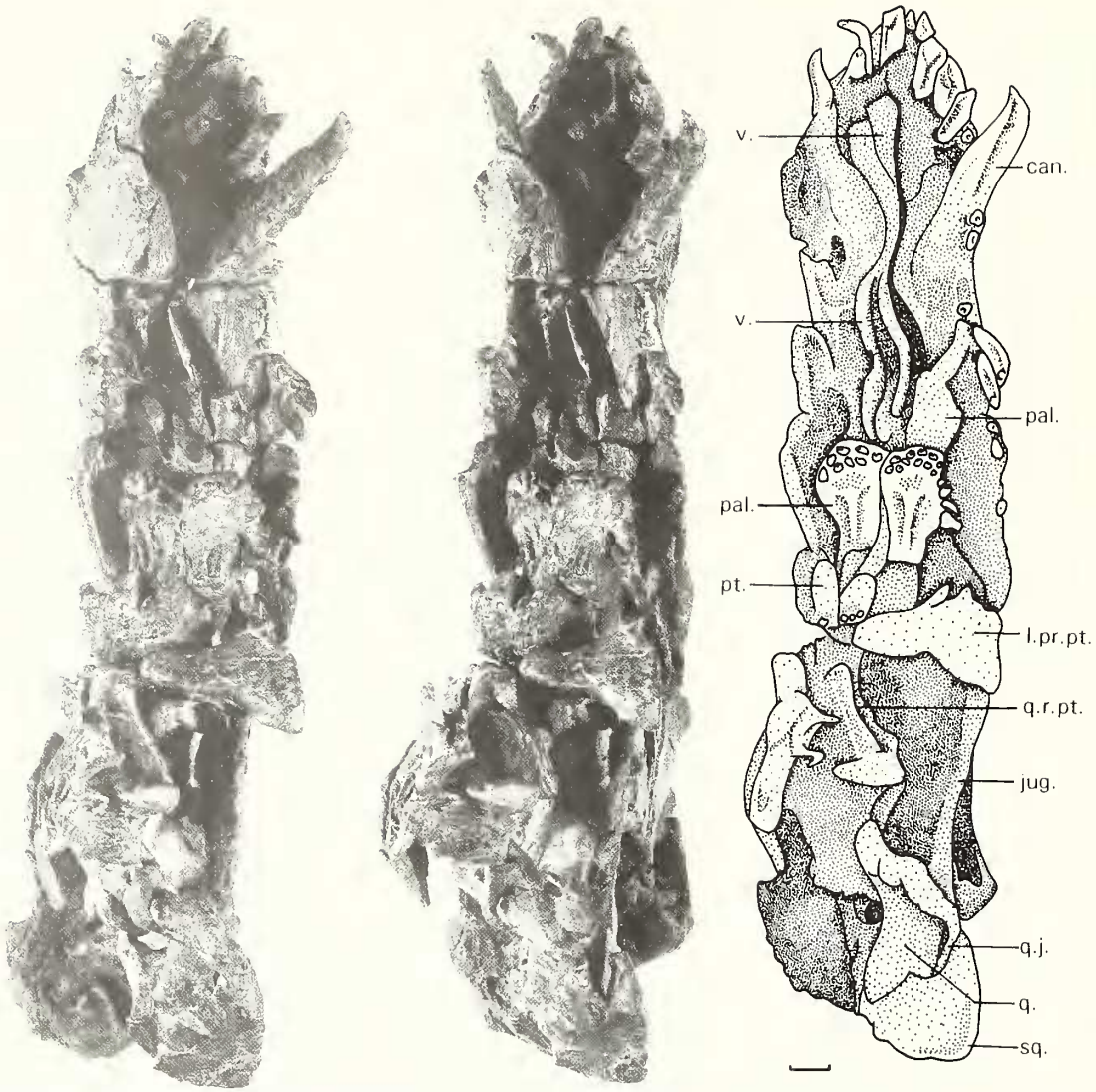
At the posterior end of the skull, the squamosal extends medially to form a plate-like bone, which meets the occipital bones on a ridge on the medial side. Dorsally it is in contact with the postorbital, and dorsomedially with the tabular. Ventrally the squamosal is in contact with the quadratojugal on the lateral side, and the quadrate on the medial side. The quadrate and quadratojugal overlie the squamosal on the anteroventral side.

The articulatory surface of the quadrate has two condyles, the medial one being smaller than the lateral one. When viewed from the posterior end, the quadrate is a broad bone which expands laterally and medially on the ventral side to form the articulatory condyles, and flares laterally on the dorsal side of the quadratojugal foramen so that the dorsal part of the bone is broad and fan-shaped. In lateral aspect, however, the quadrate is very narrow and plate-like. It is rounded on the posterior side and flattened anteriorly.

The quadratojugal is situated on the lateral side of the quadrate, and is a narrow bone when viewed from the anterior end. The ventral contact between the quadratojugal and the quadrate is situated immediately above the lateral articulatory condyle of the quadrate. The quadratojugal has an expansive footplate which extends in a medial direction beyond the limits of the quadrate foramen and overlies the posterodorsal side of the lateral quadrate articulatory condyle. On the lateral side of the foramen the quadratojugal is relatively narrow when viewed from the front but flares medially and laterally on the dorsal side of the quadratojugal foramen and here overlies the anterior side of the dorsal expansion of the quadrate.

Palate

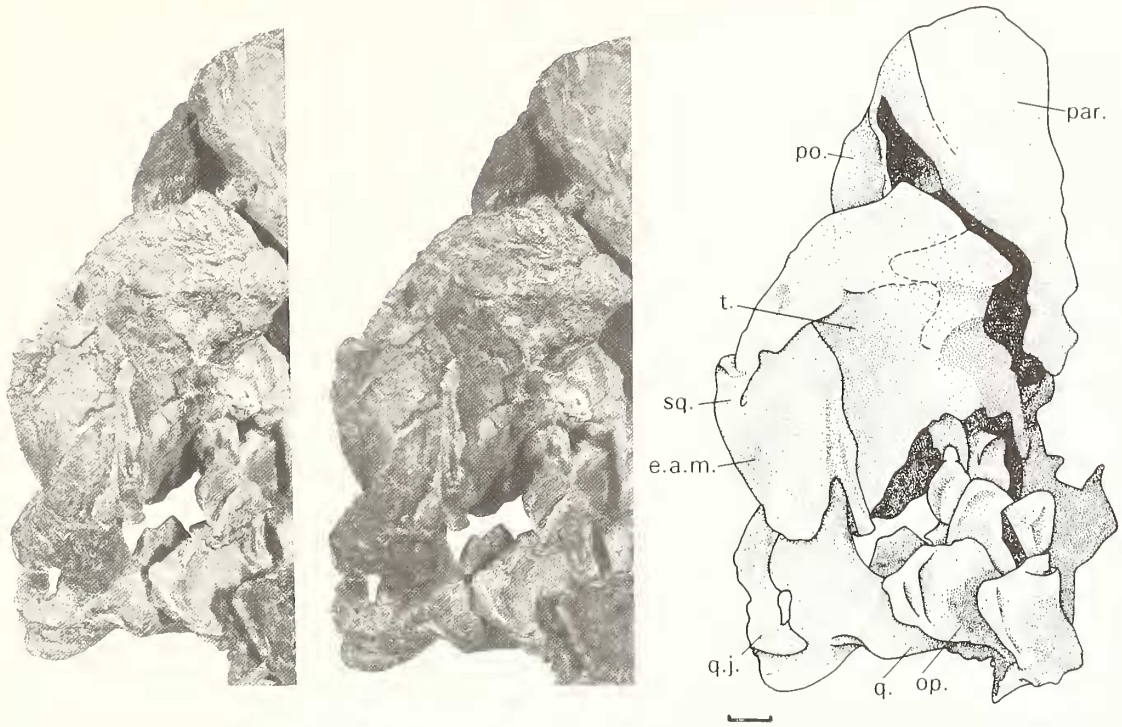
Posteriorly, the premaxilla is in sutural contact with the maxilla just in front of the canine tooth (Text-fig. 3). This suture continues medially immediately posterior to the recess in the upper jaw which accommodates the tip of the lower canine. From here the suture runs posteromedially to meet the border of the internal nares on the medial side of the canine. A longitudinal suture extends down the midline of the premaxilla.



TEXT-FIG. 3. *Australosyodon nyaphuli* gen. et sp. nov.; Prince Albert Road, South Africa; *Eodicynodon–Tapinocaninus* Assemblage zone. Holotype NMQR 3152; stereophotos and diagram of ventral view. Scale bar represents 10 mm.

Five incisor teeth are present in each premaxilla. The first incisor is relatively small, the second is slightly larger and the third is the largest. The fourth incisor is the same size as the second, and the fifth is extremely small and is situated laterally to the recess in the premaxilla which serves to accommodate the tip of the canine of the lower jaw. As the crowns of most of the incisor teeth of the upper jaw are not preserved it is difficult to determine whether small heels were initially present on their lingual side. Immediately anteromedial to the canine, the premaxilla has an indentation which accommodates the canine of the lower jaw. The suture between the premaxilla and maxilla in the palate extends medially from between the canine and fifth incisor, to meet the antero-lateral border of the internal nares at a point in line with the posterior end of the canine.

The maxilla forms the lateral border of the internal nares and apart from a single canine; it also bears twelve to thirteen postcanine teeth. The canine, which is rounded on the lateral side and flattened on the medial side,



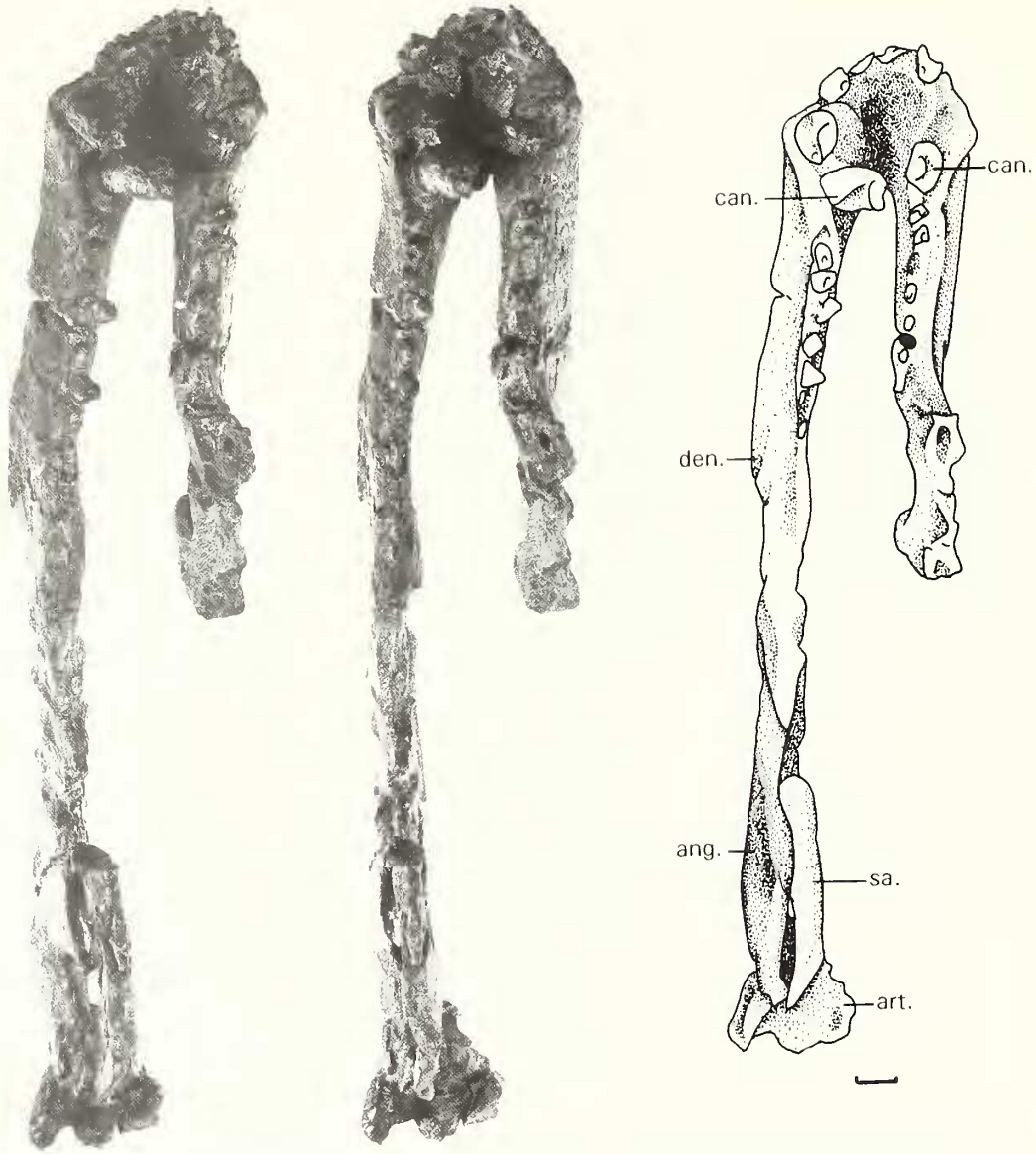
TEXT-FIG. 4. *Australosyodon nyaphuli* gen. et sp. nov.; Prince Albert Road, South Africa; *Eodicynodon–Tapinocaninus* Assemblage zone. Holotype NMQR 3152; stereophotos and diagram of occipital view. Scale bar represents 10 mm.

has a slight keel on its posterior surface. It points slightly anteriorly and laterally in its proximal regions but, closer to the tip, it curves slightly in a posterior direction as well as curving medially.

The postcanines vary in shape and form, and apart from the first two postcanines, which point slightly anteriorly, the tips of the rest point in a posterior direction. The first postcanine is situated immediately posterior to the canine, and both the first and second postcanines are relatively short and blunt. Only the roots of postcanines 3, 4 and 5 are present, and the crowns of 6, 7 and 12 are preserved as well. Judging by the anterior-posterior diameter, postcanines 6 and 7 are the largest of the postcanine teeth. The posteriormost teeth are the smallest, being even smaller than the short and blunt anteriormost teeth. The crowns are rounded on the labial side, but flattened on the lingual side. In cross-section these teeth are slightly ovoid, being more rounded anteriorly and having a slight keel on the mesial side as in *Syodon*, except that in *Syodon* the teeth are not flattened on the lingual side. The postcanine teeth of *Australosyodon* are much more slender and gracile than those of *Syodon* and *Titanophoneus*. They differ further from those of both *Syodon* and *Titanophoneus* in that they are not faceted on the point and not rounded on the lingual side.

On its posteroventral side, the maxilla is overlain by an anterior projection of the palatine. The anterior end of this projection is not preserved on the left side, but the presence of a pointed groove which tapers forwards on the ventral surface of the maxilla, is evidence that this portion of the palatine once bordered the lateral margin of the internal naris. The left side of the palate has been crushed so that it is not possible to determine the extent of the anterior projection of the palatine on this side with certainty. Posteriorly, the palatine forms a prominent ventrally projecting boss which bears twelve to fourteen teeth arranged in two concentric semicircular rows.

The vomers are paired and extend posteriorly down the midline of the palate from the premaxilla anteriorly, to meet the palatines at the posterior end of the internal nares. From here the vomers taper medially to form a pointed contact between the palatine bosses. Because the palate was distorted prior to fossilization, the vomer has been buckled. It is evident, however, that the lateral edges of the vomer curved ventrally and medially to form a prominent, ventrally protruding ridge on the lateral side of the bone, as is in *Syodon*.



TEXT-FIG. 5. *Australosyodon nyaphuli* gen. et sp. nov.; Prince Albert Road, South Africa; *Eodicynodon–Tapinocaninus* Assemblage zone. Holotype NMQR 3152; stereophotos and diagram of dorsal view of lower jaw. Scale bar represents 10 mm.

The relationship between the palatine and pterygoid is uncertain, as it appears that the palatine overlies the pterygoid on its anteroventral end. Posteromedial to the palatine boss, the pterygoid forms a smaller tooth-bearing ridge which is ovoid in shape with its pointed ends orientated anteroposteriorly. At least seven teeth are present on this ridge but their orientation cannot be determined as only the roots are preserved. A prominent ventrally projecting lateral flange of the pterygoid is present but, as the portion of the skull between the pterygoid bosses and the lateral flange of the pterygoid has been weathered away, it is not possible to determine the structure of this area of the skull. The quadrate ramus of the pterygoid flares posterolaterally at an angle of *c.* 30° to the midline. It is thin in ventral aspect, but broad when viewed laterally. The posterior

half of the quadrate ramus has broken from the anterior portion and been medially displaced. As the quadrate has been ventrally displaced in the skull, as a result of distortion, it is not possible to determine the relationship between the quadrate ramus of the pterygoid and the quadrate.

The basisphenoid has been so severely crushed that its structure is indeterminable.

Occiput

Only the left side of the occiput is preserved and, by comparison with the skulls of *Syodon* and *Titanophoneus*, it appears that the occiput of NMQR 3152 has been slightly laterally compressed (Text-fig. 4). The supraoccipital and exoccipital bones are indistinguishably fused. Posterolaterally the occipital bones form a prominent ridge where they meet the squamosal. The tabular has a broadly triangular shape, with its apex extending downwards almost as far as the ventral limits of the squamosal to form a wedge-shaped contact with the squamosal on the lateral, and the occipital bones on the medial side. Dorsolaterally the tabular is in contact with the parietal, ventrolaterally with the squamosal, and dorsomedially with the postparietal. The tabular is relatively smaller than those of *Titanophoneus* and *Anteosaurus* in that it does not extend so far ventrally.

The postparietal is incompletely preserved on the dorsal, medial, and ventromedial sides. Only the most lateral portion of the supraoccipital is preserved and is in contact with the most ventral portion of the postparietal. A sinusoidal suture separates the postparietal and tabular. Almost two-thirds of the distance up the side of the postparietal, this suture curves laterally to meet the horizontal suture which forms the border between the tabular and parietal bones. The parietal thus borders on the postparietal on its dorsal and dorsolateral sides.

Lower jaw

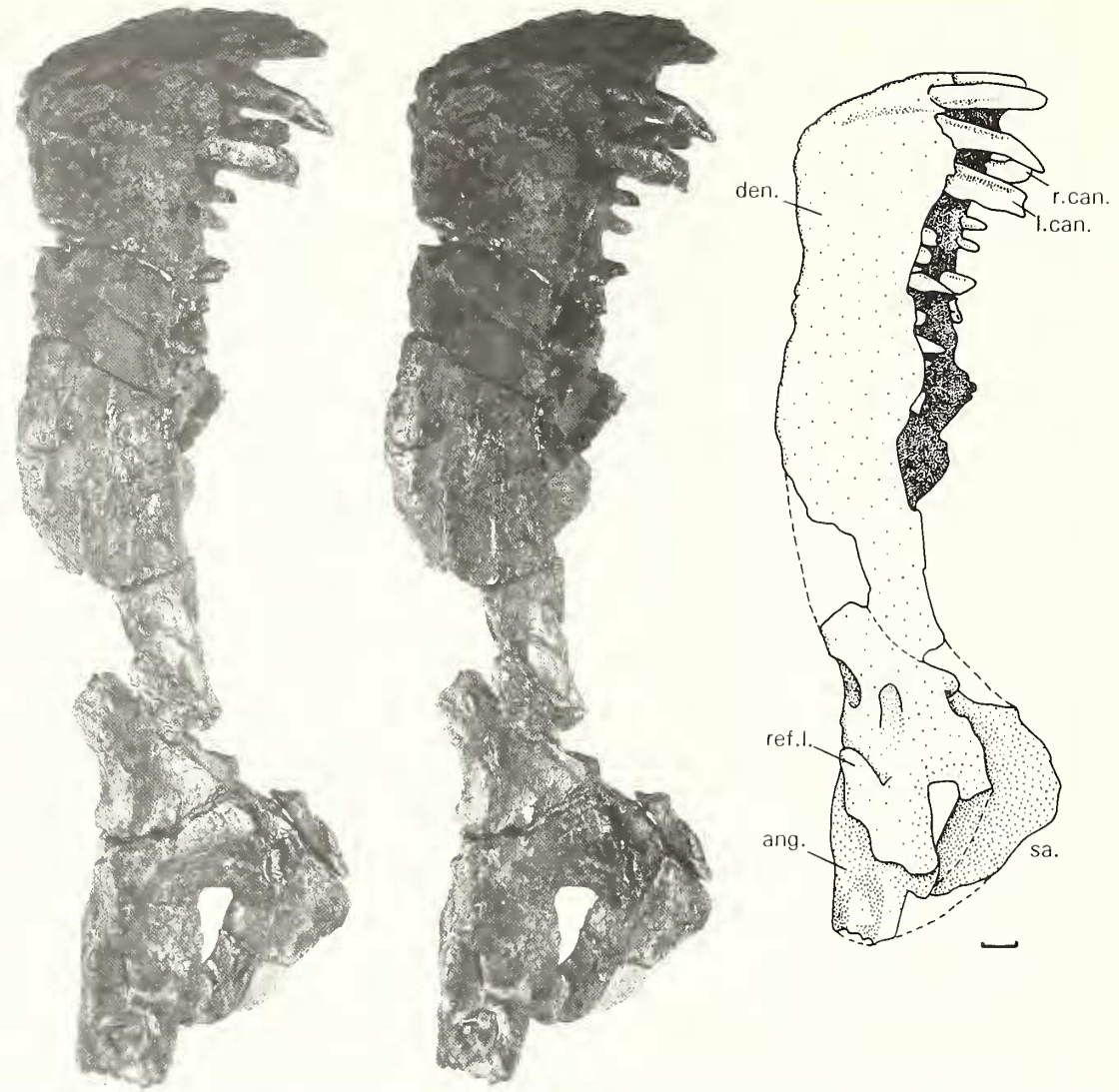
The lower jaw is relatively well preserved, with the left ramus being more complete than the right (Text-figs 5–7). Several of the teeth are in place. Portions of the ventral side of the jaw encompassing the contact area between the dentary and angular bones has been eroded away.

The dentary is the largest element of the lower jaw. Only the anterior portion of the left ramus is preserved, but the right ramus is almost complete with only the posteroventral portion weathered away. The anterior and anterolateral portion of the dentary (up to the level of the third postcanine) has a rugose surface texture which smooths out towards the posterior end. Immediately posterior to the lower canine, the lateral surface of the dentary forms a vertically orientated indentation to accommodate the upper canines which pass on the lateral side of the lower jaw when the jaws are occluded.

The dentary bears four incisors (Text-fig. 5), a single canine, and at least seven postcanines. As in *Syodon* and *Titanophoneus*, the three anteriormost incisors are relatively large. In *Australosyodon* only the root of the fourth incisor is preserved and it appears to have been smaller than the others. The tip of the first incisor is broken and badly weathered so that it is not possible to determine the morphology. Incisors 2 and 3 show signs of an incipient lingual heel. The left canine is better preserved than the right, is slightly ovoid in cross section and does not have a pronounced keel on the posterior side as is present in the upper canine. On the left ramus of the lower jaw, the postcanine dentition is complete and seven teeth are preserved, some more completely than others (Text-fig. 6). The right ramus has been distorted and the dentition is incomplete, so that it is difficult to be sure of the number of postcanines. It is estimated (counting the number of alveoli) that nine postcanines were present on this side of the jaw. When viewed from the side, all the postcanines except the last, slant slightly in a posterior direction, and have a pointed tip. The first three postcanines have a small incipient heel on the medial side, which does not appear to be present on the more posteriorly situated teeth. The last postcanine differs entirely from the rest in form. This tooth is elongated anteroposteriorly, and is flattened laterally. The crown of the tooth is not pointed but flattened. In *Syodon*, all the postcanine teeth on the lower jaw are more rounded in cross section, and have a sharp conical point. They also have slight keels (orientated anterolaterally and posteromedially) on their anterior and posterior sides. Because the jaws of the single specimen of *Titanophoneus* are tightly closed, it is not possible to determine the morphology of the crowns of the teeth.

The splenial is situated on the ventromedial side of the lower jaw, and, when viewed from the lateral side, protrudes slightly below the ventral edge of the dentary. Anteriorly the splenial is a narrow bone, which thickens posteriorly to reach its greatest thickness in the area below the fourth postcanine tooth. The posterior end of the splenial is not preserved and it is not possible to determine its relationship to the angular bone.

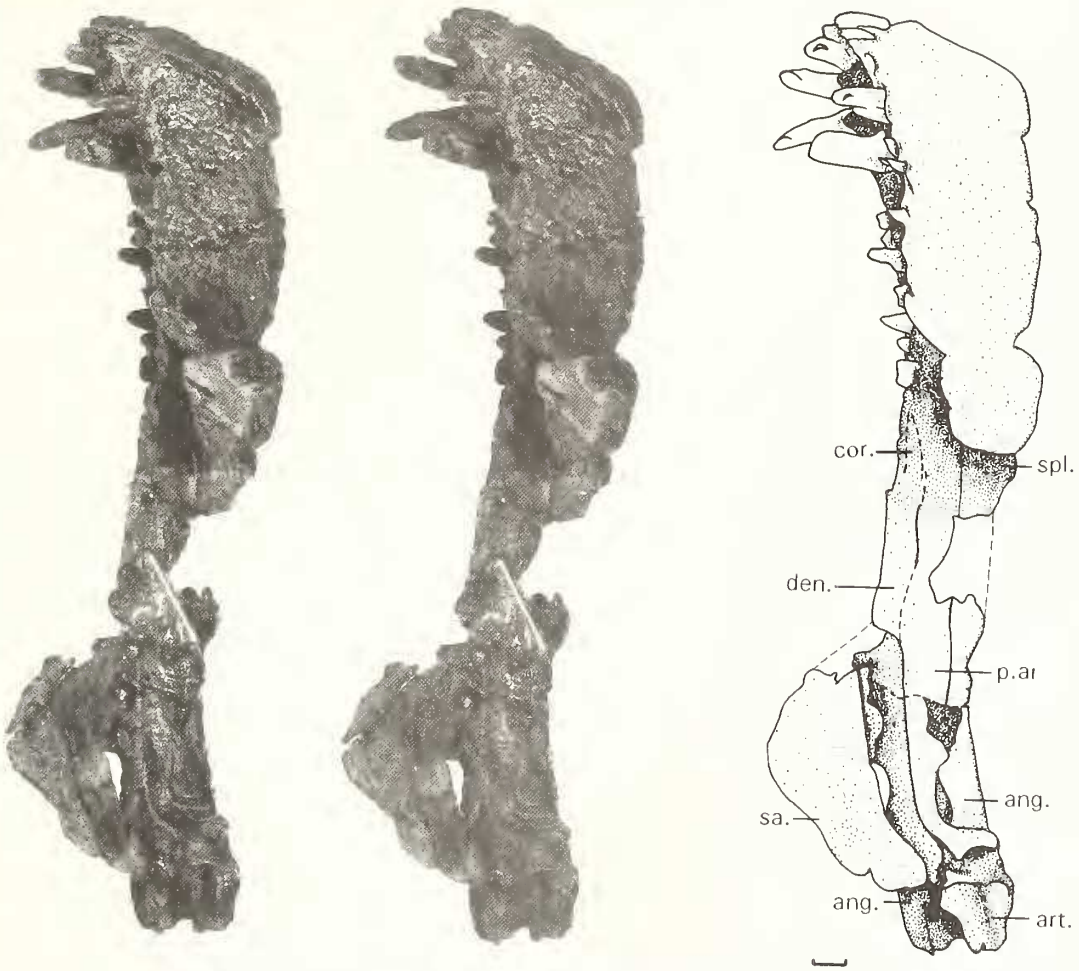
At the posterior end of the lower jaw, the angular forms the ventro-medial, ventral and most of the lateral side of the lower jaw. It tapers anteriorly to meet the dentary on the ventral side in a wedge-shaped contact



TEXT-FIG. 6. *Australosyodon nyaphuli* gen. et sp. nov.; Prince Albert Road, South Africa; *Eodicynodon–Tapinocaninus* Assemblage zone. Holotype NMQR 3152; stereophotos and diagram of lateral view of lower jaw. Scale bar represents 10 mm.

when viewed from the lateral side. The angular has its greatest exposure on the lateral side and forms a prominent reflected lamina. The posterodorsal portion of the angular is not preserved, but a semicircular grooved imprint on the lateral side of the surangular suggests the dorsal limits of this bone which reaches its greatest height below the coronoid eminence. In *Syodon* and *Titanophoneus* the angular is extremely thin in this area and so is vulnerable to destruction. The angular is also visible on the ventromedial side of the lower jaw of *Australosyodon*. The anteromedial end of this bone is not preserved so that it is not possible to determine the relationship between the angular and coronoid.

The articular is a relatively large bone bounded by the angular laterally and ventrally, and the prearticular anteriorly. The dorsal surface of the articular has a W-shape to accommodate the articulatory condyles of the quadrate.

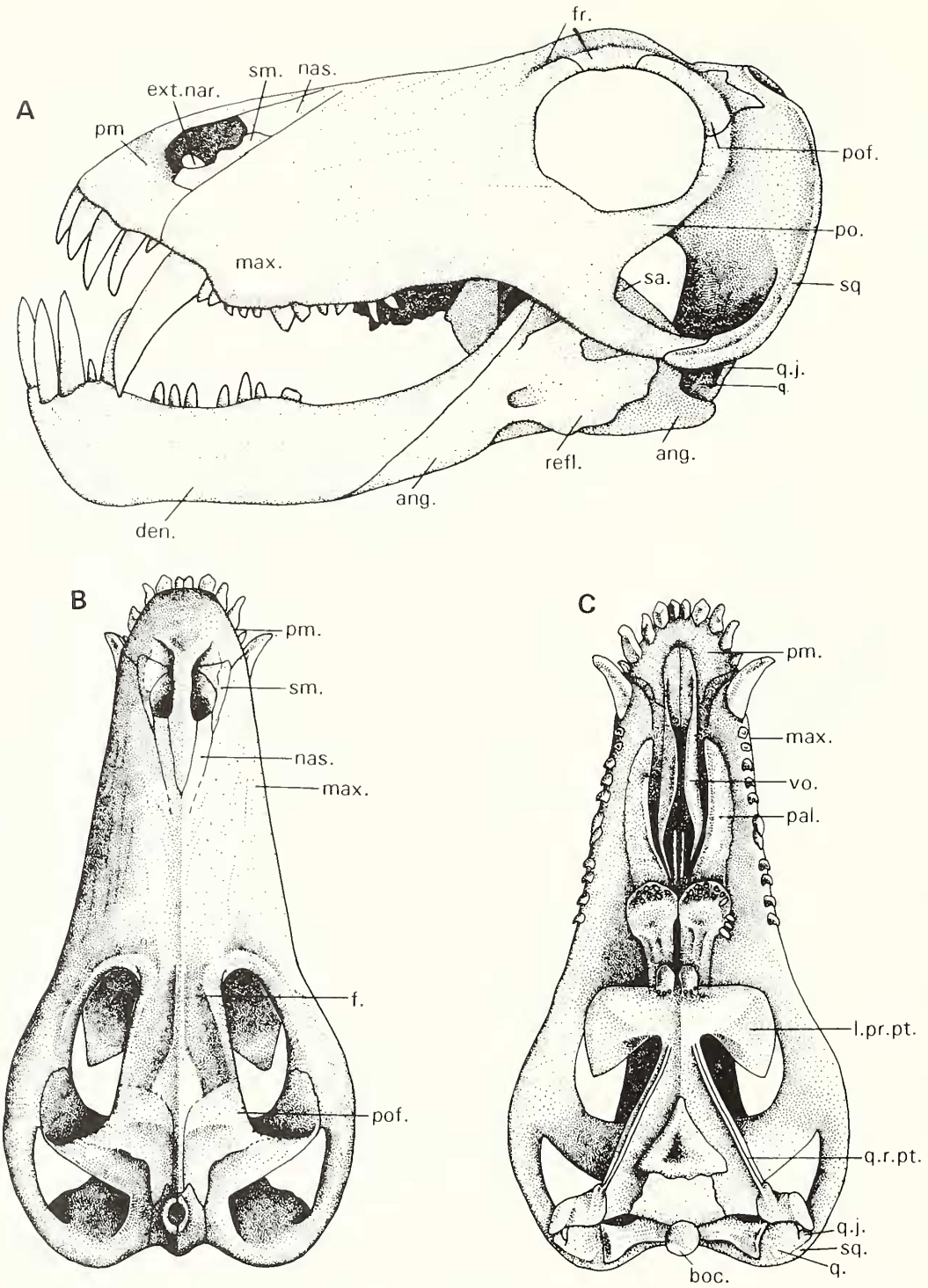


TEXT-FIG. 7. *Australosyodon nyaphuli* gen. et sp. nov.; Prince Albert Road, South Africa; *Eodicynodon–Tapinocaninus* Assemblage zone. Holotype NMQR 3152; stereophotos and diagram of medial view of lower jaw. Scale bar represents 10 mm.

The prearticular is a long, narrow bone situated on the medial side of the jaw. At its posterior end it is in sutural contact with the articular, while it meets the angular on the ventral, medial and dorsal sides. Immediately in front of the articular bone, it curves in an anterodorsal direction before extending anteriorly on the medial side of the lower jaw. Anteriorly the prearticular lies against the dentary on the dorsal and lateral sides, and appears to meet the splenial on the ventral side. The nature of the contact with the splenial is not known as the anterior portion of the prearticular is not preserved.

Prior to fossilization, the surangular was displaced from the rest of the lower jaw and lay within the temporal opening of the skull. During preparation, this portion of the lower jaw was removed from the skull and fitted back on the lower jaw, with the result that its present position on the lower jaw (as figured), is the author's interpretation of the fit. This bone forms the posterodorsal extremity of the lower jaw and is visible from both the lateral and medial sides. It is bounded by the angular on the ventral and ventro-lateral sides, and the dentary on the anterior side.

The coronoid bone has been considered to be absent in dinocephalians, but such a bone has been noted in certain dinocephalian genera (Boonstra 1936, 1956; Hopson 1991; van den Heever and Grine 1991). It is difficult to determine with certainty whether a coronoid is present in NMQR 3152, but a small bony fragment, which tapers to a point at its anterior end, is situated on the dorso-medial surface of the dentary immediately



TEXT-FIG. 8. Reconstructions of the skull of *Australosyodon nyaphuli*. gen. et sp. nov. A, lateral view; B, dorsal view; C, ventral view; ×0·4.

behind the last postcanine and is strongly suggestive of a coronoid, both in its position and size. The concave area, which has a rugose surface, is present on the posterior portion of the dentary behind the tooth row in *Syodon* and may have been the area of attachment for the coronoid bone. No coronoid or its area of attachment could be determined in *Titanophoneus*.

DISCUSSION

King (1988) considered dinocephalians with a small heel on the incisor, a slight tendency toward pachyostosis, and the jaw articulation shifted slightly forwards, to belong to the Anteosauridae. *Anteosaurus*, the only anteosaurid dinocephalian so far described from South Africa, is considered the most derived genus of this family in that the postcanine dentition is more reduced, the postorbital region of the skull is deepened producing a deeper temporal fenestra, a boss is present on the external surface of the angular (King 1988). As NMQR 3152 is clearly an anteosaurid dinocephalian but lacks the apomorphic characters of *Anteosaurus*, it is considered to be more closely allied to the primitive anteosaurid dinocephalians previously known only from Russia.

Several genera of primitive anteosaurid dinocephalians (brithopodine dinocephalians of King 1988) have been described, but many of them are based on individual postcranial elements. As the new material consists only of a skull, the genera based on postcrania alone cannot be considered for the purposes of comparison. Of the described genera, the only ones which have reasonable cranial material preserved, and can be compared with *Australosyodon* are *Archaeosyodon*, *Doliosauriscus*, *Notosyodon*, *Syodon* and *Titanophoneus*.

Archaeosyodon is represented by several incomplete skulls and fragments from the Ocher Complex. It is much larger than NMQR 3152, has teeth on the lateral flange of the pterygoid, as well as numerous teeth on the palatine and pterygoid bosses, and in these aspects alone is so different from the specimen under discussion that it need not be considered for further comparison.

Notosyodon is represented by the posterior portion of a skull, some isolated teeth, and a fragment of the left dentary, all from separate individuals. Because the posterior region of the anteosaurid skull does not have many diagnostic features, it is difficult to compare the holotype of *Notosyodon* with that of *Australosyodon*. There are, however, some obvious differences in that the dorsal edges of the orbits are more thickened (pachyostosed) than in *Australosyodon*, and the interorbital portion of the skull roof lacks the median ridge present in both *Australosyodon* and *Syodon*.

Doliosauriscus, *Syodon* and *Titanophoneus* have been well described in the literature (Orlov 1958). The degree of pachyostosis of the skull roof varies among these primitive anteosaurid genera. In *Doliosauriscus* the bone thickening is very pronounced, particularly the bones above the orbit and of the skull vault, and is very different from the new specimen. In *Titanophoneus* the thickening is restricted to the prefrontal and the dorsal border of the orbit, and in *Syodon* there is very little thickening and this is only on the dorsal border of the orbit (Orlov 1958). *Australosyodon* is similar to that of *Syodon* in that the skull roof is only slightly thickened on the dorsal border of the orbit.

As in *Syodon* and *Notosyodon*, the anterior wall of the pineal boss in *Australosyodon* is formed by the frontal and parietal bones, and not just the parietal as in *Doliosauriscus* and *Titanophoneus* (Orlov 1958). In both *Syodon* and *Australosyodon* the pineal boss forms the medial border of the area of attachment of the jaw adductor musculature, while in *Doliosauriscus* and *Titanophoneus* a ridge is present on the lateral side of the pineal boss and prevents muscle attachment on the boss. The frontal forms the anterior border of this depressed area of origin of jaw adductor musculature in *Australosyodon* and *Syodon*, but in *Doliosauriscus*, *Notosyodon* and *Titanophoneus* the frontal does not extend sufficiently far posteriorly to border on this depression. The situation in *Notosyodon*, as regards this feature, is transitional between that of *Titanophoneus* and *Syodon*.

The vomer is not completely preserved in *Doliosauriscus*, *Notosyodon* or *Titanophoneus* but in both *Australosyodon* and *Syodon*, where it is preserved, the lateral sides curve ventrally and toward the medial suture. The ventrally protruding tuberosities of the palatine of the new specimen are relatively large and prominent, and in this respect more closely resemble those of *Syodon*, rather than *Titanophoneus* or *Doliosauriscus* where the palatine bosses are smaller and less prominent

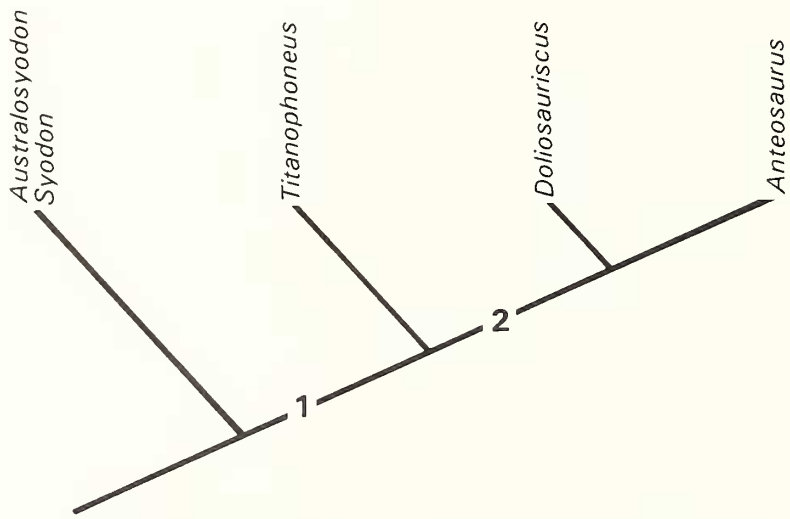
(Orlov 1958). *Australosyodon* has twelve to fourteen teeth on the palatine boss which is many more than the seven to eight of *Titanophoneus*, and is similar to the nine to thirteen of *Syodon*, and the ten to thirteen of *Doliosauriscus* (Orlov 1958).

The same trend is reflected in the ratio of the transverse diameter of the palatine bosses to that of the lateral flange of the pterygoid. This ratio is 1:3 for *Titanophoneus*, 2:3 for *Syodon* (Orlov 1958), and 2:3 for *Australosyodon*. No teeth are present on the lateral flanges of the pterygoid in *Australosyodon*. This differs from the situation in *Titanophoneus* (two large), *Syodon* (four small), and *Doliosauriscus* (three small) (Orlov 1958). The median tuberosity of the pterygoid of *Titanophoneus* and *Doliosauriscus* is small and does not bear teeth (Orlov 1958), whereas in both *Australosyodon* and *Syodon* it is large and teeth are present. The boss of *Australosyodon* is, however, much larger than that of *Syodon*.

The canine teeth of the new specimen are slightly laterally compressed and have a slight keel on the posterior side. In this respect it more closely resembles the situation in *Titanophoneus* where the canine is flattened, rather than in *Syodon* or *Doliosauriscus* where the canine is more rounded (Orlov 1958).

The shape of the postcanine teeth of *Titanophoneus* is uniform for all the teeth (Orlov 1958), whereas in the lower jaw of *Syodon* and the new specimen the crowns of the anteriormost teeth have sharp points, and the posterior two teeth have a blunt point and are wider, possibly for crushing. The length of the tooth rows of the upper and lower jaws of *Doliosauriscus* and *Titanophoneus* are the same whereas in *Syodon* and *Australosyodon* the tooth row of the upper jaw is longer than that of the lower such that the posterior postcanines of the upper jaw are unopposed (Orlov 1958).

In the lower jaw, both *Doliosauriscus* and *Titanophoneus* have a boss on the lateral surface of the angular (Hopson and Barghusen 1986). This feature is not present in either *Syodon* or *Australosyodon*, and thus seems to be coupled with the more pachyostosed skulls of *Doliosauriscus* and *Titanophoneus*.



TEXT-FIG. 9. Cladogram illustrating the relationships of anteosaurid dinocephalians (modified after Hopson and Barghusen 1986). Apomorphies for each node are: 1, lateral surface of angular has thickened area ('boss') adjacent to dentary. 2, prominent 'boss' on angular; dorsal surface of nasal, frontal and postfrontal bones pachyostosed.

CONCLUSION

It is evident that *Australosyodon* is very primitive anteosaurid dinocephalian and, as such, is the first from the southern hemisphere.

In its cranial features, *Australosyodon* most closely resembles *Syodon*, but differs in several respects: the palatine bosses of the new specimen do not protrude as far ventrally as those of *Syodon*; the anterior edge of the boss slopes gently in an antero-dorsal direction; no teeth are present on the lateral flange of the pterygoid, but at least seven teeth are present on the pterygoid boss which is larger than in *Syodon*; the canine is not rounded in cross section as in *Syodon*, but is ovoid with a slight keel which is more prominent on the posterior edge of the tooth; teeth on the maxilla and dentary less robust than those of *Syodon*; as in *Syodon* a longitudinal medial ridge extends down the midline of the frontal, but differs from that in *Syodon* in that it expands laterally to form a prominent medially situated boss above the orbits, before continuing posteriorly as a ridge right up to the pineal boss; contact of the frontal bone on the dorsal border of the orbit is slightly greater than in *Syodon*.

Syodon is considered to be the least derived genus of anteosaurid dinocephalian because it lacks a thickened area ('boss') on the angular adjacent to the dentary (Hopson and Barghusen 1986). As this feature is also absent in *Australosyodon* and in other aspects of its cranial morphology the new genus is most similar to *Syodon*, it would appear that *Australosyodon* is also one of the most primitive anteosaurid dinocephalians (Text-fig. 9). This specimen, the first skull of a primitive anteosaurid reported from outside Russia, is thus of great palaeobiogeographical consequence and, together with the rest of the primitive therapsid fauna from the same biozone, strongly suggests that the most primitive therapsids are present in South Africa as well as Russia.

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ABBREVIATIONS

ang.	angular	lac.	lachrymal	pt.	pterygoid
art.	articular	l.pr.pt.	lateral process of pterygoid	q.	quadrate
can.	canine			q.j.	quadratojugal
cm	centimeter	max.	maxilla	q.r.pt.	quadrate ramus of pterygoid
cor.	coronoid	nas.	nasal		
den.	dentary	op.	opisthotic	r.can.	right canine
e.a.m.	external auditory meatus	pal.	palatine	ref.l.	reflected lamina
		p.art.	prearticular	sa.	suragular
ext. nar.	external naris	par.	parietal	sm.	septomaxilla
fr.	frontal	p.for.	pineal foramen	spl.	splenial
i.	incisor	pmx.	premaxilla	sq.	squamosal
j.	jugal	po.	postorbital	t.	tabular
l.can.	left canine	pof.	postfrontal	v.	vomer